

# A revised familial classification for certain cirrhitoid genera (Teleostei, Percoidei Cirrhitioidea), with comments on the group's monophyly and taxonomic ranking

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P.H. GREENWOOD<sup>†</sup>

BRW 294403

Honorary Research Associate, J.L.B. Smith Institute of Ichthyology, Private Bag 1015, Grahamstown 6140, South Africa and Visiting Research Fellow, The Natural History Museum, Cromwell Road, London SW7 5BD

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**SYNOPSIS.** Previous suprageneric classifications of cirrhitoid fishes were based mainly on superficial characters. Recent anatomical studies show that five morphologically distinct types of urohyal bone occur within the group, and that on this basis certain taxa have been misplaced at both the generic and familial levels. The monophyly of the cirrhitoid fishes, tacitly assumed by previous authors, is reviewed, and an hypothesis of their monophyly erected on the basis of several synapomorphic features. It is also proposed, on the basis of those synapomorphies, that the lineage be given subordinal rank within the Perciformes.

## INTRODUCTION

During an investigation into the cranial and branchial muscles associated with feeding in certain cirrhitoid fishes from South African waters, it became apparent that five distinct morphotypes of urohyal occur within the group. Two very distinct types are found in genera currently classified as members of the Cheilodactylidae; of these two forms, one also occurs in genera referred to the family Latridae by Regan. Despite the passage of over 80 years since Regan's (1911) paper was published, it remains the most recent suprageneric classification of these fishes, which he arranged in five families, viz Cirrhitidae, Cheilodactylidae, Aplodactylidae, Chironemidae and Latridae, grouping them informally as the 'cirrhitiform percoids'.

Like its predecessor, namely Gill's more detailed paper of 1862, Regan's later analysis was based mainly on external

features. Apart from some comments by Regan on cranial features, vertebral numbers and vertebral morphology, neither paper included any other anatomical information on these fishes.

Although Regan (1911) expressed some doubts about the familial status given by him to the five generic assemblages he recognised (suggesting that subfamilial rank could be more appropriate) he did not comment on Gill's (1862) earlier classification which recognised four subfamilies within a single family, the Cirrhitoidae; indeed, and inexplicably, Regan (*op. cit.*) makes no reference at all to Gill's paper.

Gill's (*op.cit.*) four subfamilies correspond, almost entirely, to Regan's families, except that Gill's Latridinae included two genera, *Nemadactylus* Richardson, 1839, and *Cheilodactylus* Lacépède, 1803, which Regan incorporated in his family Cheilodactylidae; Gill's list of included taxa in his concept of the Latridinae also contained two genera not mentioned by Regan, despite their being recognised at that time and still being recognised today (*viz Latridopsis* Gill, 1862, and *Acantholatris* Gill, 1862).

† Dr Greenwood died 3 March 1995.

The present contribution, it is hoped, will play some part in reawakening an interest in a phylogenetically based taxonomy of Regan's 'cirrhitiform percoids', and of their interrelationships within, or perhaps outside, the Percoidei. Regan (1911) gave no formal suprafamilial ranking to his 'cirrhitiforms', but in some recent classifications (Nelson, 1994) the group has been raised to a superfamily, the Cirrhitioidea. The use of the terms 'cirrhitoid' and 'cirrhitoids' in this paper is thus to be interpreted as a reference to the superfamily and not to the suborder suggested for these fishes on p. 9.

## METHODS AND MATERIALS

Species of the percoid families Serranidae and Centropomidae served as outgroup representatives of basal members of the Percoidei. The condition and composition of the sternohyoideus muscles, and the morphology of the urohyal in these taxa were taken to represent the plesiomorphic percoid conditions.

Wherever possible, dry skeletal preparations and alizarin transparencies were examined, as were radiographs and dissections of preserved specimens.

**STUDY MATERIAL.** The symbols used in the following list are: D. Sternohyoid muscle dissected and the urohyal removed or examined *in situ*; X. Radiographed; S. Dry skeletal material examined; an asterisk following a binomen indicates that this name appears on the box housing the skeleton, and that its specific identity could not be checked on the basis of the characters preserved.

The familial grouping used in the list is that resulting from the conclusions reached in this paper, and thus differs in some respects from the classifications of Gill (1862) and Regan (1911), and in some cases that of later authors (see p. 5 relating to the species '*bergi*' and '*gayi*' previously placed in the genus *Cheilodactylus* and in the family Cheilodactylidae).

Institutional abbreviations are: BMNH, The Natural History Museum, London; DIFS, The Department of Ichthyology and Fisheries Science, Rhodes University, South Africa; RUSI, J.L.B. Smith Institute of Ichthyology, South Africa; SAM, South African Museum, Cape Town.

### STUDY MATERIAL.

#### (i) Outgroups.

Centropomidae; Glaucosomatidae; Ambassidae: The osteological and other material listed in Greenwood (1976).

Serranidae: as above, together with *Epinephalus alexandrinus* BMNH 1867.2.1: 69–72; (D).

#### (ii) Cirrhitoid fishes.

Aplodactylidae: *Aplodactylus punctatus* \* (type species of the genus): BMNH 1873.4.3: 157 (S).

*A. lophodon*: BMNH 1914.8.20: 214 (D).

Cheilodactylidae: *Cheilodactylus fasciatus* (type species of the genus): 3 specimens, DIFS unregistered (D).

*C. fuscus*: 1 specimen, DIFS unregistered (D).

*C. pixi*: 6 specimens, DIFS unregistered (D).

2 specimens, DIFS unregistered (S).

4 'paperfish' larvae, 44–50 mm standard length, RUSI 19842 (D).

1 'paperfish' larva, 44 mm standard length, RUSI 19842 (S).

*C. zonatus*: BMNH 1907.12.23: 238 (S).

*Chirodactylus brachydactylus*: 3 specimens, DIFS unregistered (D).

2 specimens, DIFS unregistered (S).

2 'paperfish' larvae, 33 & 38 mm standard length. RUSI, unregistered (D).

*C. grandis*: 1 'paperfish' larva, 57 mm standard length. RUSI 18404 (D).

*Dactylophora nigricans*\*: BMNH 1869.2.24:8 (S).

Chironemidae: *Chironemus marmoratus*\*: BMNH 1871.3.29: 28 (S).

*Chironemus marmoratus*: BMNH 1861.11.7: 6 (D).

Cirrhitidae: *Amblycirrhitus pinos*: 2 alizarin preparations ex BMNH 1976.7.14: 453–7 (S).

*Amblycirrhitus pinos*: BMNH 1984.7.16: 96 (D).

*Cirrhitus maculatus*\*: BMNH unregistered (S).

*Cirrhitichthys oxycephalus*: RUSI 11658; BMNH 1929.9.20: 8 (D).

*Cirrhitichthys oxycephalus*: BMNH 1908.3.23: 77–79 (X).

*Cyprinocirrhitus polyactis*: RUSI 12339 (D).

*Gymnocirrhitus arcatus* (type species of the genus): BMNH 1965.12.20: 10 (D).

*Gymnocirrhitus arcatus*\*: BMNH unregistered, collected by Richardson (S).

*Gymnocirrhitus arcatus*: BMNH 1865.3.2: 82–83 (X).

*Oxycirrhitus typus* (type species of the genus): BMNH 1929.6.12: 2 (D).

*Paracirrhitus forsteri*: BMNH 1852.9.13: 119 (S)

*Paracirrhitus forsteri*: BMNH 1969.7.16: 28–32; one specimen (D).

Latridae: *Acantholatris bergi* BMNH 1936.18.26: 439 (D) & (X).

*Acantholatris gayi*: BMNH 1879.5.14: 278; 1890.2.26: 49 (D) & (X).

*Acantholatris monodactylus* (type species of the genus): BMNH 1960.1.8: 6–13; one (D), all (X).

*Acantholatris monodactylus*: BMNH unregistered, ex Gough Isl.; 2 specimens, both (S).

*Acantholatris monodactylus*: RUSI 33484; 33485; 33624 (D).

*Latridopsis ciliaris* (type species of the genus): BMNH 1872.7.1: 32 (S).

*Latridopsis ciliaris*: BMNH 1873.12.13: 55 (D) & (X).

*Latris lineata*: BMNH 1855.9.19: 124 (D).

*Latris lineata*: SAM 22623 (D).

*Mendosoma lineatum* (type species of the genus): BMNH 1960.1.8: 14–21; one (D), all (X).

*Mendosoma lineatum*: RUSI 33613; 33625 (D).

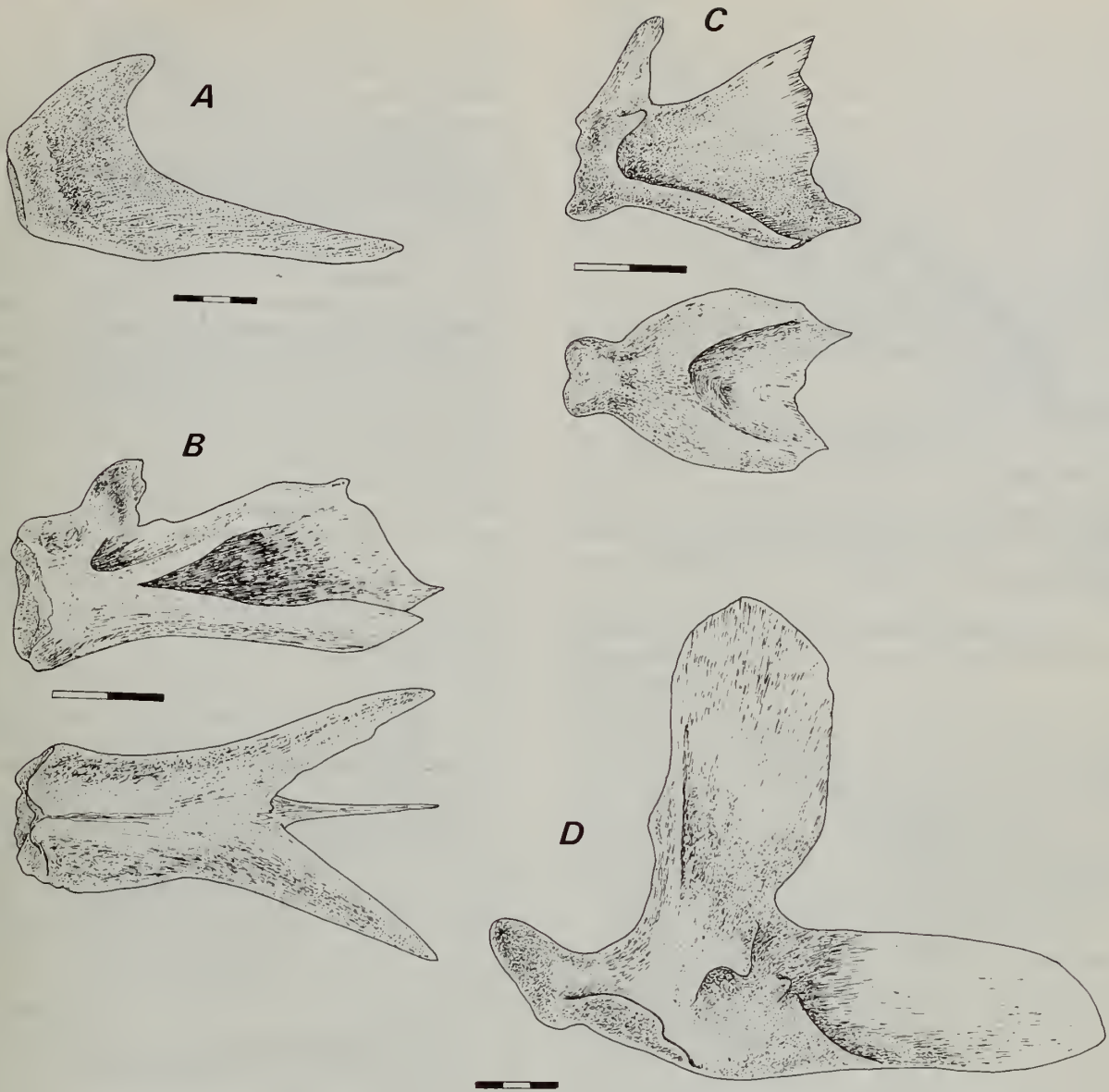
*Nemadactylus macropterus*: BMNH 1855.9.19: 314 (X).

*Nemadactylus macropterus*: BMNH 1872.7.1: 21 (D) & (X).

## Urohyal morphology and the suprageneric classification of cirrhitoid fishes, particularly the genus *Acantholatris* and species currently referred to the genus *Nemadactylus*

Within the cirrhitoid fishes, five morphologically distinct types of urohyal can be recognised (Figs 1 & 2). Since each





**Fig. 1** The urohyal of: A. *Paracirrhites forsteri*; Cirrhitidae; left lateral view (BMNH 1852.9.13: 119). B. *Chironemus marmoratus*; Chironemidae; left lateral and ventral views. (BMNH 1871.3.29:28). C. *Aplodactylus punctatus*; Aplodactylidae; left lateral and ventral views. (BMNH 1873.4.3: 157). D. *Dactylophora nigricans*; Cheilodactylidae; left lateral view. (BMNH 1869.2.24:8). Relative to other figures, this bone has been rotated through 90° to the left; arrow indicates dorsal prominence. Scale in millimetres. Drawn by Gordon Howes.

type can be correlated with one of the five family groups recognised by Regan (1911), these will be referred to as the cirrhitid, latrid, chironemid, aplodactylid and cheilodactylid types respectively.

The cirrhitid type (Fig. 1A) appears to be a plesiomorphic form, one fundamentally similar to that found in several basal percoids (see Kusaka, 1974; also personal observations).

The latrid urohyal (Fig. 2) differs markedly from the cirrhitid type, and also shows slightly more intrafamilial variation, particularly with regard to its posterior margin's degree of indentation, the extent to which the ventral margin is produced bilaterally into a narrow or broader shelf, the extent to which the bone is produced ventrally, and whether

the bone's upper margin is sharp or somewhat flattened. Like the cirrhitid type, the latrid urohyal is also of a plesiomorphic form, one occurring in such basal percoids as the Serranidae and Centropomidae (Kusaka, 1974; Greenwood, 1976: 39, fig. 21, and other personal observations).

Departure from the basal percoid form of urohyal is most pronounced in the chironemid, aplodactylid and cheilodactylid types of bone. In chironemids (Fig. 1B) the bone is shallow, the ventral margin greatly flattened and expanded bilaterally to form a broad shelf, while the dorsal margin is also noticeably flattened and bilaterally produced into a shelf, albeit one relatively narrower than that on the ventral aspect of the bone; when compared with the urohyal in cirrhitids,

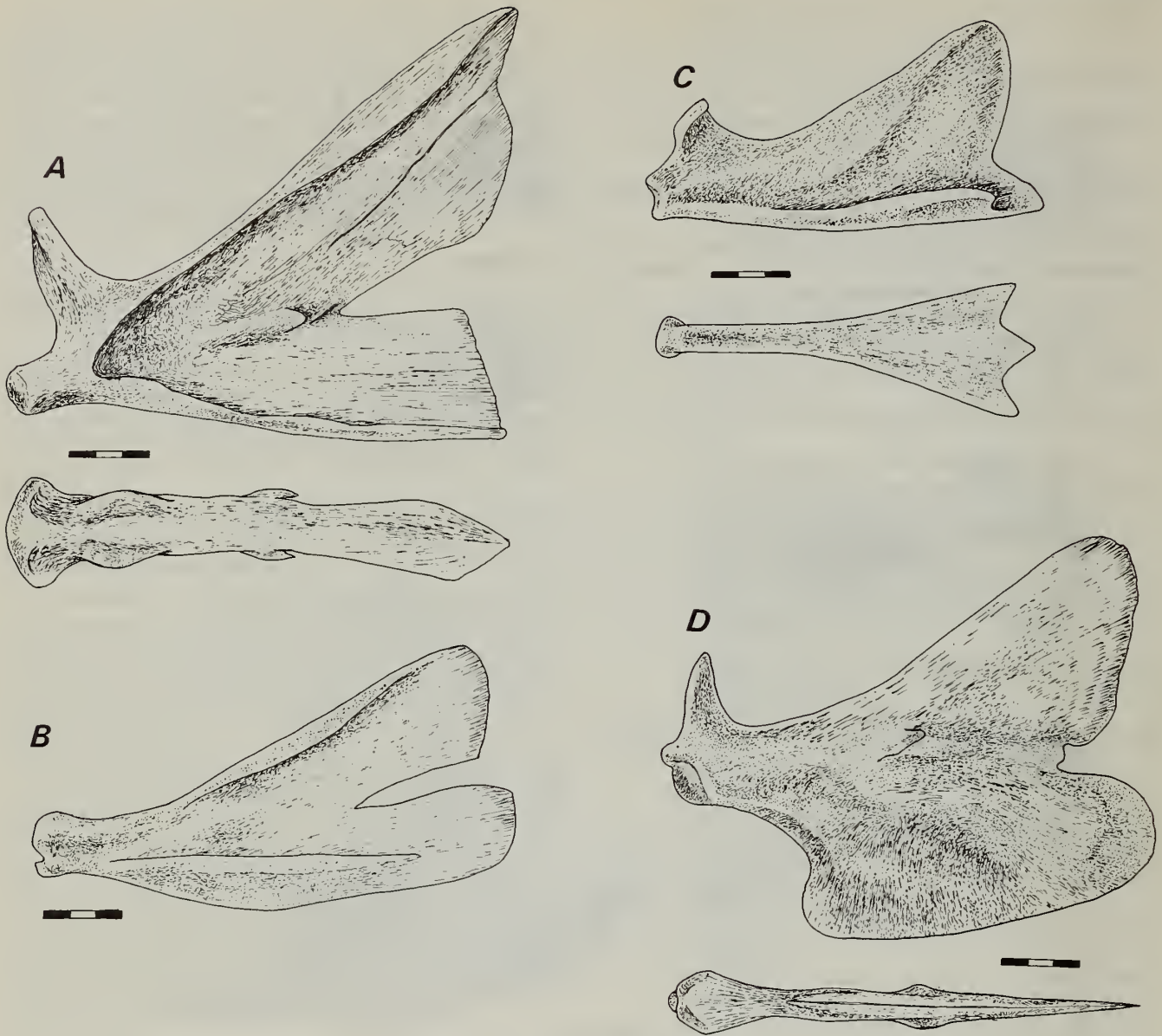


Fig. 2 The urohyal of four latrid species. A. *Acantholatris monodactylus* (BMNH unregistered; ex Gough Island); left lateral and ventral views. B. *Latris lineata* (BMNH 1855.9.19:194); left lateral view. C. *Mendosoma lineatum* (BMNH 1960.1.8:14-21); left lateral and ventral views. D. *Latridopsis ciliaris* (BMNH 1872.7.1:31); left lateral and ventral views. Scale in millimetres. Drawn by Gordon Howes.

the chironomid type is relatively foreshortened (cf Figs 1A & 1B).

A pronounced ventral shelf and overall foreshortening of the bone is also characteristic of the aplodactylid urohyal (Fig. 1C), but in this type the bone is relatively deeper than is the chironomid urohyal, and the dorsal surface is produced into only a narrow shelf.

When compared with all other types, the cheilodactylid urohyal (Fig. 1D) is very distinctive. In lateral view it has virtually the shape of an arrow-head with its tip directed anteriorly, and with the two arms meeting at the somewhat thickened apex from which a dorsally directed process arises. The anterior edges of both arms are slightly broadened to form a very narrow bilateral shelf that does not quite extend to the posterior tip of either arm. Although, morphogenetically, the cheilodactylid type of urohyal could be derived

from a latrid type by a marked anterior extension and deepening of the latter's posterior indentation, coupled with an increase in the angle subtended by the two arms so formed, the two morphotypes are readily distinguishable. Interestingly, the urohyal in the so-called 'paperfish' juvenile stage (see p. 7) of a 44 mm standard length *Cheilodactylus pixi* Smith, 1980, resembles that of the latrid type more closely than does this bone in larger specimens; nevertheless, the upper and lower arms of the urohyal in the 'paperfish' stage are more widely separated, the division between them extends further anteriorly, and the anterior body of the bone is less compressed and more barrel-like than that in any of the adult latrid urohyals I have examined.

In his monograph on urohyal bones Kusaka (1974) described and illustrates this bone in *Goniistius zonatus* (Cuv., 1839), a taxon now, and previously (Gill, 1862),



referred to the family Cheilodactylidae (see Allen & Heemstra, 1976, for comments on the status of this genus; also p. 6 below). Kusaka, however, lists the species under the heading Aplodactylidae. The bone depicted is certainly of the cheilodactylid type and not of the aplodactylid type, and I presume Kusaka's placing the species in the Aplodactylidae is a *lapsus*. This author (*op. cit.*) also figured and described the urohyal from a specimen supposedly of *Cirrhitichthys aureus* Temm. & Schl., 1843 (Cirrhitidae). Unfortunately I have not been able to examine a specimen of this species, but the bone illustrated (and described as 'shaped like a standing rat') is unlike that in any cirrhitoid taxon I have examined, particularly amongst members of the Cirrhitidae and even in a taxon such as *Oxychirrhites typus* Bleeker, 1857, whose elongate and tubular snout is an unusual morphotype within both the Cirrhitidae and the cirrhitoids as a whole. If Kusaka's figure and description are accurate and the specimen was correctly identified, then a sixth and highly distinctive form of urohyal, one far removed from that of other cirrhitids must be recognised, and the higher taxonomic position of its possessor or possessor be reconsidered (assuming, that is, the bone Kusaka examined was not teratological or damaged during preparation).

A typical cheilodactylid urohyal (Fig. 1D) occurs in all members of the family (*sensu* Regan [1911] and subsequent authors) I have examined apart from *Nemadactylus* and members of the genus *Acantholatris*, viz the type species *A. monodactylus* (Carmichael, 1818), and the species *A. gayi* (Kner, 1869) and *A. bergi* (Norman, 1937).

Parenthetically it should be noted that *A. gayi* and *A. bergi* were both placed in the genus *Cheilodactylus*, and the family Cheilodactylidae, by Norman (1937). The former species was later transferred by Fowler (1945) to the genus *Acantholatris*, with no explanation given for the change, but was retained in the family Cheilodactylidae. Neither author appears to have been aware, however, that Gill (1862) had included *Acantholatris* in his subfamily Latridinae. Mann (1954: 266) followed Fowler's generic and familial placing of *A. gayi*, and listed the species *bergi* under *Acantholatris* in the index to that publication. The reader is there referred to page 266 of the text. No mention is made of *A. bergi* on that page, but on page 85 (*op. cit.*) *Acantholatris bergi* Norman (the author's name not enclosed in brackets) is listed amongst the 'Invasores del Atlantico'. Mann (*op. cit.*) is thus the first author to employ this particular combination of names for the species. As noted earlier (p. 1) Regan did not include *Acantholatris* in any of his cirrhitiform families.

### The familial classification of *Acantholatris* Gill, 1862 and *Nemadactylus*

The urohyal in all three *Acantholatris* species examined, and in *Nemadactylus macropterus*, is virtually identical and differs markedly from that in the cheilodactylids, cirrhitids, aplodactylids and chironemids (see pp. 2–5 and *cf* Fig. 1 with Fig. 2A). Instead, it resembles the latrid type, both in detail and in its gross morphology (*cf* Figs. 2A, B and C), especially in its fan-like outline. This marked difference would suggest that the latrid genera (as listed in Regan, 1911), together with *Acantholatris* and *Nemadactylus* shared a recent common ancestry distinct from that of the cheilodactylids. It also suggests that the phyletic relationships of the two groups are obscured by uniting the cheilodactylids with the latrids in a

single subfamily, as did Gill (1862).

Thus, in my view, based essentially on their urohyal morphology and not negated by other characters (see, however, the pectoral fin character discussed below), *Acantholatris* and *Nemadactylus* should be included in the family Latridae, currently comprising species of the genera *Latris*, *Latridopsis* and *Mendosoma*, the latter recently shown to be monotypic by Gon & Heemstra (1987). In addition to the urohyal characters, the genera listed above lack a suborbital shelf, which in cheilodactylids is a prominent feature formed from the posterior upper margin of the lachrymal bone and the entire upper margins of the second and third suborbitals. Also, unlike cheilodactylids, these genera have the basal scaly sheath to the soft dorsal fin somewhat higher and thus more prominent than that at the base of the spinous part of the fin.

As in cheilodactylids, the latrids (here taken to include *Acantholatris* and *Nemadactylus*) have 35 vertebrae (14 abdominal + 21 caudal elements including the urostylar element; data from radiographs and dry skeletons listed on p. 2). To judge from the dry skeletal and dissected material available to me, parapophyses are present on all precaudal centra in both families, and no ribs are sessile.

### Possible lineages within the Latridae as now expanded to include the genera *Acantholatris* and *Nemadactylus*

*Acantholatris* and *Nemadactylus* differ noticeably from *Latris*, *Latridopsis* and *Mendosoma* in having one of the lower, unbranched pectoral rays (*i.e.* the fifth, sixth or seventh ray from the bottom of the series) greatly elongated, its tip, which extends beyond the fin's margin, reaching to at least the level of the anus and sometimes as far as the midpoint of the anal fin.

There are also differences in the following features:

- (i) In scale size, as shown by lateral-line scale counts. In *Latris*, *Latridopsis* and *Mendosoma* these range from 112 to 120 in the two former taxa, and from 68–78 in *Mendosoma* (data from Last *et. al.*, 1983; Gon & Heemstra, 1987; pers. obs.). In *Nemadactylus macropterus* the count is 59 or 60, and in other species 47–68 (pers. obs.; Last *et. al.*, 1983) and in *Acantholatris monodactylus*, *A. bergi* and *A. gayi* the range is from 50–60 (Norman, 1937; pers. obs.).
- (ii) Anal fin length. In *Latris*, *Latridopsis* and *Mendosoma*, the number of branched anal rays ranges from 17–35 (the lowest counts occurring in *Mendosoma*, viz. 17–21, whereas in *Acantholatris* species and *Nemadactylus macropterus* the range is from 12–15, and other species of the genus, 16–19 (sources as above).

Pending a detailed generic revision of the various taxa involved, especially the several Australian and New Zealand species currently referred to the genus *Nemadactylus* it would be premature to formally recognise the two groups as, for instance, tribes or subfamilies of the Latridae, although phylogenetically some split seems to have occurred within the lineage.

The condition of the pectoral fin in the *Latris-Latridopsis-Mendosoma* group of latrids provides something of a puzzle since these taxa are the only cirrhitiforms not showing any marked elongation of the uppermost unbranched ray in the lower section of the pectoral fin, nor, as in most other

cirrhitoids, do any of these rays clearly extend beyond the fin membrane, and none is markedly thickened. In having the lowermost 5–9 rays unbranched, these fishes are, however, typically cirrhitoid. This latter condition can be considered one of the synapomorphies uniting cirrhitoid fishes.

A typically derived pectoral fin configuration occurs in the Cirrhitidae, yet the family would appear to be the least derived of all cirrhitoid taxa (see p. 8). In contrast, except for the condition of the pectoral fin, members of the *Latris-Latridopsis-Mendosoma* assemblage within the Latridae share with *Acantholatris* and *Nemadactylus*, and with the cheilodactylids, aplodactylids and chironemids, the derived condition for all the osteological and myological features discussed on page 5. That being so, it is unlikely that the pectoral fin form in *Latris*, *Latridopsis* and *Mendosoma* can be interpreted as a true retention of the plesiomorph condition. If that was the case, then the derived condition must have evolved more than once within the cirrhitoids. A more parsimonious solution to the problem therefore, would, be to interpret the pectoral fin form in *Latris*, *Latridopsis* and *Mendosoma* as a secondary reversal to a seemingly more plesiomorphic condition than is found in any other cirrhitiforms, including the family with the greatest number of plesiomorphic features, the Cirrhitidae (see p. 8).

The geographical distribution of the two groups within the Latridae has an interesting pattern. Of the taxa in the long-finned assemblage, *Nemadactylus* (see p. 5) occurs only in Australia, Tasmania and New Zealand, thus overlapping the entire range of *Latridopsis* a member of the short-finned group and one restricted to that region; it overlaps in part (New Zealand and Tasmania) that of the widely distributed *Mendosoma lineatum*, also a member of the short-finned group, and in part, that of *Latris*, another member of the short-finned group (Australia; New Zealand; Gough and Tristan da Cunha islands; Vema Seamount; St Paul and Amsterdam islands). The other long-finned taxon, *Acantholatris*, does not occur in Australasia, but has a wide western distribution, including St Paul, Amsterdam, and Gough Islands, Tristan da Cunha, Vema Seamount Chile, Juan Fernandez and the western coast of South America from Rio de Janeiro southwards. This distribution thus widely overlaps that of the short-finned, monotypic genus *Mendosoma lineatum*, viz St Paul, Amsterdam and Gough islands, the coast of Chile and, as noted above, New Zealand and Tasmania (the latter being areas where *Acantholatris* does not occur); data from Norman, 1937; Fowler, 1945; Mann, 1954; Smith 1984; Last *et. al.*, 1983; Gon & Heemstra, 1987; Paulin *et. al.* 1989; Andrew & Hecht, 1992; Andrew, pers.comm., 1993).

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## TAXONOMIC AND PHYLOGENETIC CONCLUSIONS

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### Taxonomy

The material studied indicates, on osteological and myological grounds (p. 5), that the species currently named *Nemadactylus macropterus* (the type species of Gill's (1862) genus *Dactylopagrus*; see Wheeler, 1986) should be classified in the Latridae and not the Cheilodactylidae as it is at present.

The genus *Acantholatris* Gill (1862, type species *Chaetodon monodactylus* Carmichael, 1818), was overlooked by Regan (1911) in his synoptic review of cirrhitoid families, but is currently placed in the family Cheilodactylidae (see p. 5). However, on the basis of its urohyal morphology, and its lacking a suborbital shelf (see p. 5) the genus should be classified in the Latridae. Regan (1911) differentiated the Latridae from the Cheilodactylidae on the basis of the latrids having feeble, unbranched pectoral rays that are not produced beyond the fin's margin, and by their lacking a suborbital shelf; in other features he noted that the two families are similar. With the inclusion of *Acantholatris* and *Nemadactylus* in the Latridae the nature of the pectoral fin no longer serves as a differentiating feature (see p. 5), the principal diagnostic characters for the family now lying in the form of the urohyal bone, the absence of a suborbital shelf, and in the more prominent arrangement of the basal sheathing scales of the soft dorsal fin (see p. 5).

Gill's (1862) suprageneric classification included *Nemadactylus* as a division – Nematodactyli – of his subfamily Latridinae, in which subfamily but as another division to which he gave the name Latridae he also included *Latris*, *Latridopsis*, *Mendosoma*, *Acantholatris*, *Chirodactylus*, *Cheilodactylus* and *Goniistius*. Regan (1911) on the other hand, but without reference to Gill's paper, treated the latter author's four subfamilies as families, and recognised a fifth, the Cheilodactylidae, for two genera, viz *Cheilodactylus* and *Nemadactylus*; no mention is made in Regan's paper of the other taxa in Gill's Latridinae except for *Latris* and *Mendosoma*, which Regan retained in his family Latridae.

The evidence presented here (pp. 2–5), especially that based on urohyal morphology, would support Regan's (1911) classification with regard to the separation of *Cheilodactylus* (and, although not mentioned by Regan, *Chirodactylus* and *Goniistius*) from the other taxa included in Gill's Latridinae, and would support the inclusion of all three taxa in one family, the Cheilodactylidae. The same evidence would also support Gill's inclusion of *Latris*, *Latridopsis*, *Acantholatris*, *Mendosoma* and *Nemadactylus* in a single suprageneric taxon. Since Regan's (1911) familial ranking has been accepted and used since that time, and until contraindicative evidence is available to suggest otherwise, that ranking (i.e. Latridae) is retained.

The anatomical and other features used in this paper (pp. 2–5) would support the recognition of Gill's (1862) and Regan's (1911) other suprageneric lineages, again, for the reasons given above, as families and not subfamilies, viz. the Cirrhitidae, Aplodactylidae (Gill's Haplodactylinae) and Chironemidae.

At an intrafamilial taxonomic level, Allen & Heemstra (1976) note that 'The currently accepted classification of the Cheilodactylidae . . . is most unsatisfactory' a sentiment I would not only endorse, but would extend to other cirrhitiform families as well. In part this situation has resulted from the use of mainly superficial characters, with little or no attention paid to anatomical features, especially myological and osteological ones. Thus on those grounds I cannot agree with Allen & Heemstra's (*op.cit.*) treating *Acantholatris* as a subjective synonym of *Cheilodactylus* and its consequent placement in the Cheilodactylidae (see above, p. 5). However, at least on the characters and specimens I have examined, I would endorse their synonymy of Whitley's (1957) genus *Morwong* (type species *Cheilodactylus fuscus* Castelnau, 1879) with *Cheilodactylus*.



### The cirrhitoids as a monophyletic lineage

On the basis of several apparently synapomorphic characteristics (see below) the cirrhitoids would seem to be a monophyletic lineage, a conclusion implied by both Gill (1862) and Regan (1911) who described the group as a 'natural' one but gave no reasons for that conclusion. The derived characters on which I would base an hypothesised monophyly of the cirrhitoids are, taken in conjunction, a reduced number (15) of principal caudal fin rays, the unbranched lowermost five to nine rays in the pectoral fin (usually with their tips produced beyond the fin membrane), the lower part of each cleithrum greatly expanded anteroposteriorly and meeting its antimere in a deep, carinate symphysis, an increased number of vertebrae relative to other percoids (26–35, comprising 10–16 abdominal and 15–21 caudal elements), and the presence, ventrally, in subadults of a peculiar, lipoid-filled sac (Fig. 3), free from the overlying hypaxial muscles, and extending from the urohyal, to which it is attached, to the anus, with the lipoidal material apparently contained in hexagonal compartments.

To the best of my knowledge, this lipoid sac has not previously been noted as a feature of subadult cirrhitoid fishes, nor indeed of any other perciforms except the stichaeid *Lumpenus maculatus* (see Falk-Petersen *et al.*, 1984). I first observed it in small specimens (the so-called 'paperfish' stage) of *Cheilodactylus pixi* ca 43 to 44 mm standard length (Fig. 3), where its presence results in the 'pouter-pigeon'-like ventral profile of the paperfish stage in this and other cirrhitoid species (see photographs in Whitley, 1957; Allen & Heemstra, 1976, and Nielsen, 1963). Subsequent dissections revealed a lipoid sac in members

of all but two of the cirrhitoid families I have dissected (see p. 2). The exceptions are a chironemid, *Chironemus marmoratus* Günther, 1860 (160 mm standard length) and an aplodactylid, *Aplodactylus lophodon* Günther, 1859 (180 mm S.L.). Since, however, the sac is a juvenile (*i.e.* sub-adult) feature in the other taxa, and the exceptional specimens were, to judge from their gonadal development, young adults, I suspect that it would also be present in smaller specimens of these species. In *Cheilodactylus pixi*, for example, the sac is well-developed in a specimen of 44 mm standard length, but has disappeared in one of 46 mm. Likewise, in *Chirodactylus brachydactylus* (Cuv., 1830), it is present in a fish of 38 mm standard length, but absent in one of 42 mm. The presence of a lipoid sac in specimens from 128 to 243 mm standard length of other species (referred in the current literature to the Latridae and Cheilodactylidae) whose maximum adult lengths are from 50 cm to one metre, suggests that the size at which the lipoid sac disappears is positively correlated with that at which members of a species become adult. This supposition is borne out by the presence of the sac in a juvenile *Chirodactylus grandis* (Günther, 1860) of 57 mm standard length, a species whose adults reach a length of one metre, whereas it has disappeared, at a length of 42 mm, in young *Chirodactylus brachydactylus*, whose adults reach a length of 40 cm. Again, it is present in a specimen of *Acantholatris monodactylus* 243 mm S.L.; adults of this species attain a standard length of at least 65 cm. Thus, the sac's apparent absence in chironemids and aplodactylids could be artefactual, and related to the size-range of the specimens I was able to examine.

It is hoped to carry out a more detailed examination of the lipoid sac when specimens suitably fixed for detailed histo-



Fig. 3 *Chirodactylus pixi*, 49 mm standard length (RUSI 19842) in right lateral view; partially dissected, and with the greater part of the pectoral and the entire pelvic fin removed. The large anterior portion of the lipoid sac (LS) is clearly visible; part of its posterior portion is also visible (x). Throughout its length, the wall of the sac, unlike the muscles above it, is heavily peppered with melanophores.

logical and histochemical study are available.

### Intragroup relationships within the cirrhitoids, and the ranking of the group

Within the cirrhitoids, the Cirrhitidae should be ranked as the most plesiomorphic taxon, a view seemingly implicit in Regan's (1911) diagram of relationships. My reasons for giving the family this ranking are based on urohyal form, the low vertebral count (26–28) relative to that in other families, the absence of parapophyses on the first three abdominal vertebrae, sessile ribs associated with these vertebrae, the presence of 3 predorsal bones (2 in the other cirrhitoids radiographed or dissected) and the presence of a suborbital shelf (which, however, is also developed in the Cheilodactylidae [but see below]). Furthermore, the Cirrhitidae are the only cirrhitoids with a basal percoid type of myotome arrangement in the sternohyoideus muscle, a feature not previously noted. That is, one in which the three pairs of hypaxial myomeres forming the sternohyoideus muscle are all arranged in a vertical series, with the first block covering the anterior part of the urohyal (Fig. 4A). Members of all other cirrhitoid families, in contrast, have the first (*i.e.* anterior) hypaxial myotome of each side displaced ventrally so that it now lies medially and horizontally (not, as in cirrhitids, laterally and vertically) to form, with its antimere, a ventral muscle, paired in most species but in some with the left and right parts fused over most of their lengths to form a single median muscle (Fig. 4B). Single or paired, this ventro-medial component of the sternohyoideus runs from the urohyal tip to the prominent ventral projection at the symphysis of the left

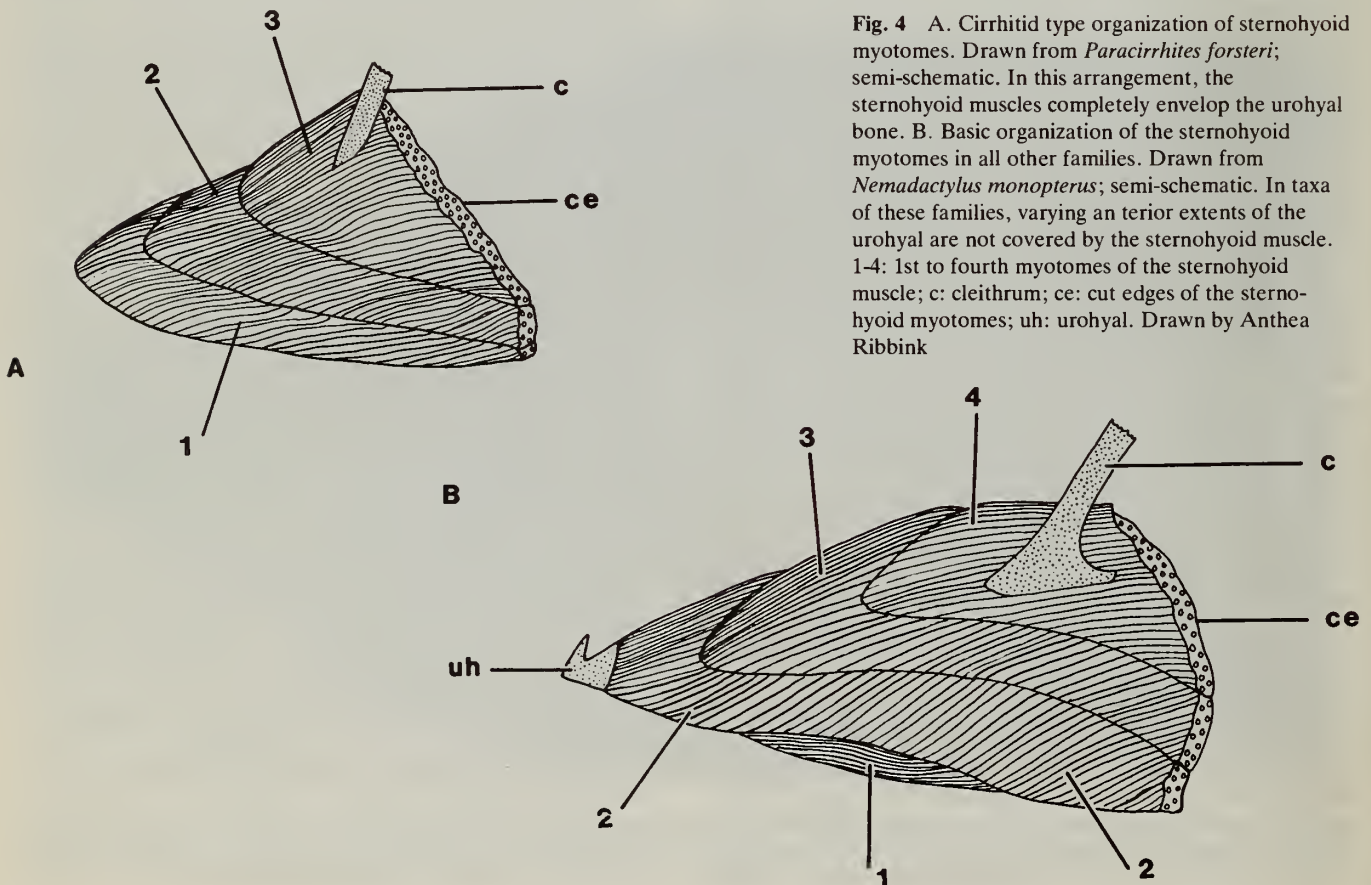
and right cleithra, its origin thus being immediately before that of the anterior infracarinalis muscle insertion.

In both the Cirrhitidae and in the other families, the sternohyoideus myotomes, except the horizontal first myotome in the latter group, are chevron-shaped with the apex directed anteriorly. However, in the latrids, cheilodactylids, chironemids and aplodactylids, the angle between the upper and lower arms of the chevron is more acute, and the lower arm is relatively longer than in cirrhitids.

Judging from the rather scant literature on the sternohyoideus muscle in teleosts (see Winterbottom, 1974), and from a personal knowledge of the situation in percoids, the condition of the muscle in the Cirrhitidae should be ranked as plesiomorphic, that in the other cirrhitoid families as derived and possibly a unifying synapomorphy for the Aplodactylidae, Chironemidae, Latridae and Cheilodactylidae within the lineage.

In Regan's (1911) figure of cirrhitoid intrarelationshi ps referred to above, the Cirrhitidae occupy a basal (*i.e.* stem position) and are linked, on the one hand to the Chironemidae and Aplodactylidae, and on the other to the Cheilodactylidae and Latridae (the generic composition of the families being those given by Regan). No reasons were provided by Regan for these supposed relationships, which presumably were based mainly on superficial characters as well as a few anatomical ones. With the anatomical information now available a different scheme of intragroup relationships at the family level can be proposed (see Fig. 5, and Table 1).

In this scheme, apomorphic features (see Table 1) are taken to be: (i) The derived form of urohyal, of which there are three distinct types (see p. 3). (ii) The presence of a



**Fig. 4** A. Cirrhitid type organization of sternohyoideus myotomes. Drawn from *Paracirrhites forsteri*; semi-schematic. In this arrangement, the sternohyoideus muscles completely envelop the urohyal bone. B. Basic organization of the sternohyoideus myotomes in all other families. Drawn from *Nemadactylus monopecterus*; semi-schematic. In taxa of these families, varying anterior extents of the urohyal are not covered by the sternohyoideus muscle. 1-4: 1st to fourth myotomes of the sternohyoideus muscle; c: cleithrum; ce: cut edges of the sternohyoideus myotomes; uh: urohyal. Drawn by Anthea Ribbink



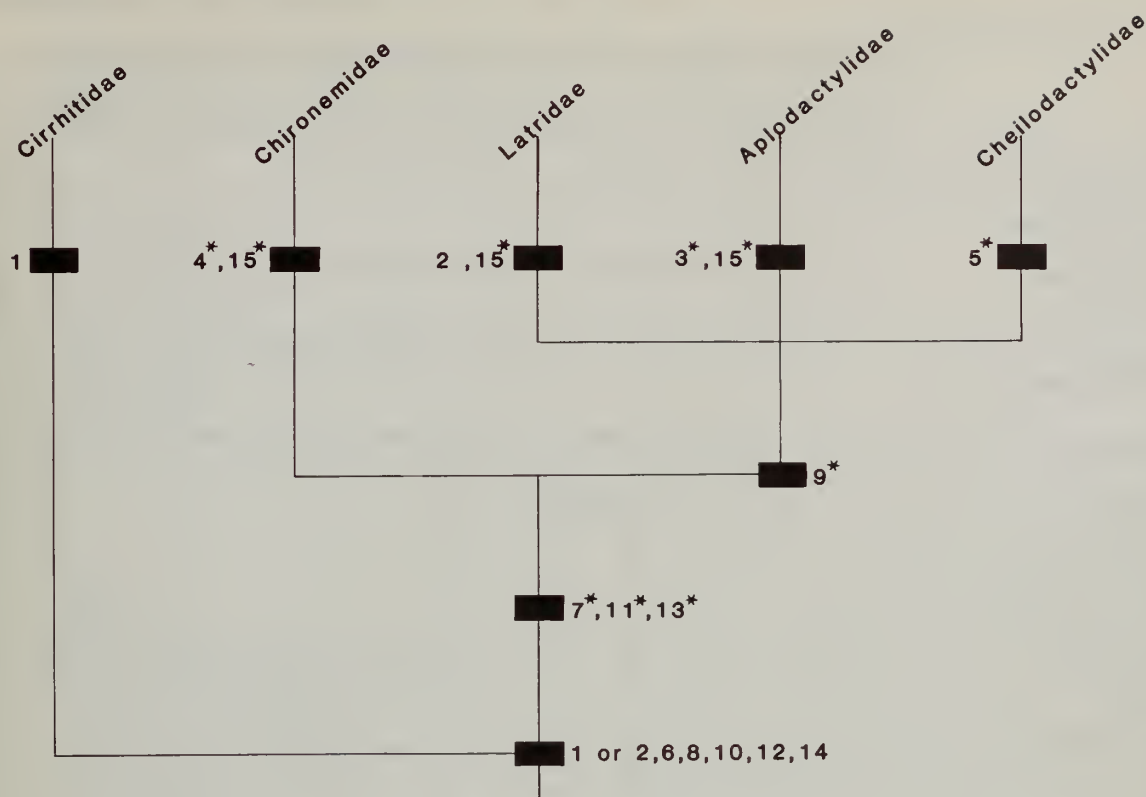


Fig. 5 Tentative scheme of phyletic relationships within the Cirrhitoidae. Asterisks indicate apomorphic characters (see also Table 1). Since both the cirrhitid (1) and latrid (2) condition of the urohyal are rated as plesiomorphic, that bone in the common ancestor of all lineages is taken to be 1 or 2.

derived myotomal arrangement of the sternohyoideus muscles (p. 8). (iii) More than 28 vertebrae. (iv) Parapophyses developed on the first three abdominal vertebrae, with the first pleural rib associated with the second or third vertebrae. (v) Predorsal bones reduced to 2. The three different types of derived urohyal morphology (pp. 2–5) (*ie* in chironemids, aplodactylids and cheilodactylids) are each taken to be independently evolved apomorphies. Relationships (Fig. ) suggested by these data are: (i) That the cirrhitids are the plesiomorph sister group to the other four families combined. (ii) The chironemids are the sister taxon of the aplodactylids, latrids and cheilodactylids combined, and that for the moment this assemblage should be treated as an unresolved trichotomy since no two lineages uniquely share a recognisable synapomorphic feature. For example, the urohyal in the latrids is of a basal percoid type, and although that bone in the cheilodactylids and aplodactylids is highly derived, each is unique to the families respectively. The cheilodactylids it will be noted, retain the plesiomorphic suborbital shelf, whereas it is lost in the latrids and aplodactylids (and in the chironemid lineage as well). The value of this feature as an indicator of relationship, however, is problematical because it involves a loss (and not an acquisition) in the lineages concerned. Clearly, a greater number and variety of characters must be sampled and their polarity determined before this hypothesis of cirrhitoid intrarelationships can be improved and the trichotomy resolved.

The same reservation would apply before any sister-group hypothesis can be erected regarding the relationships of the cirrhitoids within the Percomorpha. However, based on the

synapomorphic features discussed (above pp. 6–7) it seems reasonable to hypothesize that the five families comprising the lineage, given informal ranking as the 'cirrhitiform percoids' by Regan (1911), and suprafamilial status by recent authors (Nelson, 1994), should be elevated to subordinal status (Cirrhitoidae) within the Perciformes.

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Table 1 Data matrix and characters.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<b>Cirrhitidae</b>															
<i>Amblycirrhitus pinos</i>	+	0	0	0	0	+	0	+	0	+	0	+	0	+	0
<i>Cirrhitus maculatus</i>	+	0	0	0	0	+	0	+	0	+	0	+	0	+	0
<i>Cirrhitichthys oxycephalus</i>	+	0	0	0	0	+	0	+	0	+	0	+	0	+	0
<i>Cyprinocirrhites polyactis</i>	+	0	0	0	0	+	0	+	0	+	0	+	0	+	0
<i>Gymnocirrhites arcatus</i>	+	0	0	0	0	+	0	+	0	+	0	+	0	+	0
<i>Oxycirrhites typus</i>	+	0	0	0	0	+	0	+	0	+	0	+	0	+	0
<i>Paracirrhites forsteri</i>	+	0	0	0	0	+	0	+	0	+	0	+	0	+	0
<b>Chironemidae</b>															
<i>Chironemus marmoratus</i>	0	0	0	+	0	0	+	+	0	0	+	0	+	0	+
<b>Latridae</b>															
<i>Acantholatris bergi</i>	0	+	0	0	0	0	+	0	+	0	+	0	+	0	+
<i>A. gayi</i>	0	+	0	0	0	0	+	0	+	0	+	0	+	0	+
<i>A. monodactylus</i>	0	+	0	0	0	0	+	0	+	0	+	0	+	0	+
<i>Latridopsis ciliaris</i>	0	+	0	0	0	0	+	0	+	0	+	0	+	0	+
<i>Latris lineata</i>	0	+	0	0	0	0	+	0	+	0	+	0	+	0	+
<i>Mendosoma lineatum</i>	0	+	0	0	0	0	+	0	+	0	+	0	+	0	+
<i>Nemadactylus macropterus</i>	0	+	0	0	0	0	+	0	+	0	+	0	+	0	+
<b>Aplodactylidae</b>															
<i>Aplodactylus punctatus</i>	0	0	+	0	0	0	+	0	+	0	+	0	+	0	+
<i>A. lophodon</i>	0	0	+	0	0	0	+	0	+	0	+	0	+	0	+
<b>Cheilodactylidae</b>															
<i>Cheilodactylus fasciatus</i>	0	0	0	0	+	0	+	0	+	0	+	0	+	+	0
<i>C. fuscus</i>	0	0	0	0	+	0	+	0	+	0	+	0	+	+	0
<i>C. pixi</i>	0	0	0	0	+	0	+	0	+	0	+	0	+	+	0
<i>C. zonatus</i>	0	0	0	0	+	0	+	0	+	0	+	0	+	+	0
<i>Chirodactylus brachydactylus</i>	0	0	0	0	+	0	+	0	+	0	+	0	+	+	0
<i>C. grandis</i>	0	0	0	0	+	0	+	0	+	0	+	0	+	+	0
<i>Dactylophora nigricans</i>	0	0	0	0	+	0	+	0	+	0	+	0	+	+	0

Characters: 1. Cirrhitid-type urohyal (*i.e.* of a basal percoid type, but one differing from the latrid condition); 2. Latrid-type urohyal (*i.e.* of basal percoid type; see 1); \*3. Aplodactylid-type urohyal; \*4. Chironemid-type urohyal; \*5. Cheilodactylid-type urohyal; 6. Less than 28 vertebrae; \*7. More than 28 vertebrae; 8. Parapophyses not developed on the first three (sometimes 4) abdominal vertebrae, but sessile pleural ribs on one or two of these centra; \*9. Parapophyses developed on the first three abdominal vertebrae. No sessile pleural ribs; 1st pleural rib articulating with the parapophyses of the third abdominal vertebrae; 10. Three predorsal bones; \*11. Two predorsal bones; 12. Basal percoid-type of sternohyoid muscle; \*13. Derived condition of the sternohyoid muscle; 14. Suborbital shelf present; \*15. Suborbital shelf absent. Asterisk indicates an apomorphic feature.

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